

UNION OF *BRADBURIA* WITH *CHRYSOPSIS* (ASTERACEAE: ASTEREAEE),
WITH A PHYLOGENETIC HYPOTHESIS FOR *CHRYSOPSIS*

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ABSTRACT

The monotypic genus *Bradburia* (*B. hirtella* Torrey & Gray) is merged with *Chrysopsis* (as *C. texana* *nom. nov.*), enlarging the latter to eleven species. Within *Chrysopsis*, *C. texana* and *C. pilosa* are sister species, based on a set of distinctive features common to both taxa. Both species are the westernmost of the genus and (as *Chrysopsis* sect. *Bradburia* *comb. et stat. nov.*) they form a group phyletically coordinate with the other species, which are centered in the southeastern United States. A phylogenetic hypothesis is presented for all species of *Chrysopsis*; the genera most closely related to it are *Osbertia* and *Noticastrum*.

KEY WORDS: *Bradburia*, *Chrysopsis*, *Osbertia*, *Noticastrum*, Asteraceae, Astereae

The taxonomic history of the monotypic genus *Bradburia* Torrey & Gray has been summarized by Semple & Chinnappa (1984). Essentially, it has been recognized as closely related to the genera *Heterotheca* Cass. and *Chrysopsis* (Nutt.) Ell., but it differs prominently from both in its sterile disc flowers. The dimorphic achenes of *Heterotheca* (sensu Semple 1977; Semple *et al.* 1980) have been noted by some authors as similar, and perhaps homologous, to those of *Bradburia*, but Semple (1981) has observed that a closer relationship exists between *Bradburia* and *Chrysopsis*, in his more restricted view of the latter. Semple (1981, p. 339), indeed, placed the relationship so close that he hypothesized that some isolated, immediate precursors of *C. pilosa* Nutt. "ultimately evolved into *Bradburia hirtella*."

Semple & Chinnappa (1984, p. 95) noted that "While *Bradburia hirtella* could be transferred to *Chrysopsis*, the distinctive staminate florets of the former are considered sufficient to separate the two at the generic level." Later in

the same paper (p. 100), they commented that "The distinctive achene morphology, somewhat different flavonoid pattern, and karyotype support maintenance of *Bradburia* as a genus separate from *Chrysopsis*." The data from the flavonoid studies, however, were not presented in their study, and its authors noted in the same paper (p. 95) that "Flavonoid patterns in the two genera were similar but did not confirm or refute a close relationship."

CHROMOSOMES

Detailed studies of meiotic pairing in *Chrysopsis* hybrids (Semple & Chinnappa 1980a) and of chromosome numbers and karyotypes (Semple & Chinnappa 1980b) showed that four basic karyotypes exist within *Chrysopsis*: the $x = 4$ of *C. pilosa*, the $x = 4$ of *C. mariana* (L.) Ell., the $x = 5$ of the majority of the species, and the $x = 9$ of *C. gossypina* (Michx.) Ell. The latter comprises "little more than a combination of the $x = 5$ karyotype and the $x = 4$ *mariana* karyotype and was therefore of allopolyploid origin." (1980b, p. 164). These two studies provided convincing evidence of strong homology between the $x = 4$ *mariana* and the $x = 5$ karyotypes, the former probably derived by loss of chromosome "V" of the $x = 5$ set, with transfer of portions of that chromosome to both chromosomes "II" and "III" of the $x = 4$ *mariana* set. Semple & Chinnappa (1980b, p. 170) hypothesized that the "evolution of the $x = 4$ [*pilosa*] karyotype from the $x = 4$ [*mariana*] karyotype resulted in a considerable increase in asymmetry and an increase in the number of acrocentric homologues" but noted (p. 168) that "no clear homologies [between these two $x = 4$ karyotypes] are suggested by chromosome size and centromere position."

Plants of *Bradburia* have a chromosome number of $n = 3$ over most of the geographic range of the species, but Semple & Chinnappa (1984) reported the significant discovery of an individual with $n = 4$ from the southwesternmost portion of the range. They presented a detailed study of the karyotypes of the two *Bradburia* cytotypes and an artificially synthesized hybrid between the two. In comparing the $n = 4$ chromosome complement of *Bradburia* with that of *Chrysopsis pilosa*, they observed (p. 100) that "if the large pair of the *C. pilosa* karyotype was more metacentric, then the karyotype would be superficially very similar to that of the $n = 4$ karyotype of *Bradburia*." Based on their very clear photographs and diagrams, the phrase "superficially very similar" could be replaced by "virtually identical." Semple & Chinnappa (p. 99) further noted that comparison of their karyotypes "suggests a possible origin of *Bradburia* from an early ancestor of *C. pilosa*." They did not offer a precise hypothesis of how the $n = 3$ complement originated from the $n = 4$, but clearly the two may be interpreted as homologous.

MORPHOLOGY

Phylogenetic analyses of the goldenaster lineage (Nesom 1991a) and of the genus *Chrysopsis* (see details below) indicate that *Bradburia* is closely related to *Chrysopsis*, based on their thin walled and vitreous upper cells of the Type A trichomes, and distinctive achene morphology (obovate, with thick, buried ribs). Among the species of *Chrysopsis*, it is similar to *C. pilosa* in its chromosome number, karyotype (see discussion above), annual duration, spring flowering, long flowering branches, Type A trichomes with the distal cells thin walled but not elongated into a flagelliform terminal portion, phyllaries with broad scarious margins, lack of characteristically large, elongated crystals in the tissues of the disc corolla throat, sharp pointed sweeping hairs on the disc style branches, and ray corollas remaining straight rather than coiling. Together these similarities provide evidence that the two taxa are related as sister species.

Despite its close relationship to *Chrysopsis pilosa*, *Bradburia* differs from it in a number of features. The difference that has been heavily emphasized is the sterility of disc ovaries and concomitant reduction of the disc pappus to two awns. Additionally, the ray achenes of *Bradburia* are 3 sided, the outer face distinctly broadened (vs. merely 2 sided in *C. pilosa*), with an outer pappus composed of a whorl of relatively inconspicuous, short bristles and setae (vs. a whorl of broad scales); the pappus bristles of *Bradburia* are distinctly flattened and characteristically reddish near the base (vs. terete and tawny); the leaves of *Bradburia* are narrow at the base and strictly sessile (vs. basally broadened and subclasping); the heads of the glandular (Type C) trichomes are broader (5-8 cells across vs. 3-5 cells); and the phyllaries are essentially glabrous (vs. distinctly hairy glandular). Attempts to cross *Bradburia* with *C. pilosa* have been unsuccessful (Semple & Chinnappa 1984), and populations of the two species are sometimes intimately intermixed in nature (Nesom personal observ.).

While the differences that separate *Bradburia* from *Chrysopsis pilosa* are at least as great as those that distinguish most other species of *Chrysopsis*, Semple (1981, p. 338) noted that *C. pilosa* itself is "the most divergent species [of the genus] in terms of morphology, chemistry, and cytology." Further, *C. pilosa* and *Bradburia* are so distinct as a pair that *C. pilosa* might justifiably be transferred to *Bradburia*, but the similarity in achene morphology between them and the other species of *Chrysopsis* strongly suggests that the group as a whole is monophyletic and should stand as a single genus. Artificially produced hybrids between *C. pilosa* and *C. gossypina* (Semple 1981) emphasize a significant degree of genetic similarity between the two segments of the genus. No one has suggested that *C. pilosa* be formally recognized apart from the other species of the genus; if it is taxonomically treated as *Chrysopsis*, then so should *Bradburia*. The close relationship between these two species, apart

from the rest of the genus, is formalized in the nomenclature below.

Chrysopsis sect. **Bradburia** (Torrey & Gray) Nesom, *comb. et stat. nov.*

BASIONYM: *Bradburia* Torrey & Gray, *Fl. N. Amer.* 2:250. 1842.

Species included: *C. pilosa* Nutt. and the type species:

Chrysopsis texana Nesom, *nom. nov.* BASIONYM: *Bradburia hirtella*

Torrey & Gray, *Fl. N. Amer.* 2:250. 1842; not *Chrysopsis hirtella* DC.,

1836. TYPE: UNITED STATES. Texas: [no other data], *Drummond*

134 (HOLOTYPE: not seen; Probable isotype: LL!).

CLADISTIC ANALYSIS

In a broader cladistic study that includes all of the goldenasters (Nesom 1991a), *Osbertia* ($x = 5$) E. Greene of México and Central America and *Noticastrum* DC. ($x = 9$) of South America are hypothesized to be the closest relatives of *Chrysopsis* (including *Bradburia*), based on their relatively long, smooth, thin walled, and vitreous Type A trichomes. In order to determine the phylogenetic position of *Bradburia*, it has been included in a phylogenetic analysis of the species of *Chrysopsis*, with the assumption that such a group is holophyletic only with the inclusion of *Bradburia*. The closely related goldenaster genus *Heterotheca* has been added as part of the outgroup to clarify some of the character state polarities.

Studies of microcharacters were made with a compound microscope using epidermal "skims" with a razor from stems and slides of dissected flowers mounted in Hoyer's Medium. A list of specimens from which slides have been made is deposited at TEX; all voucher specimens are deposited in TEX. All specimens examined and scored of *Bradburia* presumably have a chromosome number of $n = 3$. Characters and character states used in the analysis are given in Table 1; coding for the individual taxa are in Table 2; discussion of variability in the characters used is provided in the Appendix. The data were analyzed using PAUP (Swofford 1985) with Wagner parsimony. *Chrysopsis gossypina* was not included in the analysis, since it apparently is of hybrid origin (Semple 1980b); its position relative to the other species is shown on the cladogram following Semple (1981).

A single shortest tree of 42 steps (Fig. 1) accounts for the distribution of character states among the taxa included in the analysis. *Chrysopsis texana* (*Bradburia*) and *C. pilosa* (sect. *Bradburia*) are geographically the westernmost of the genus and form a clade phyletically coordinate with the other species (sect. *Chrysopsis*), which are centered in the southeastern United States. In contrast to Semple (1981), who placed the ancestor of the whole genus in

TABLE 1. Characters and character states

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1. Chromosome number, (0) $n = 4$ or 3 , the "pilosa" karyotype, or $n = 9$ (1) $n = 5$ or 4 , the "Chrysopsis" karyotype
 2. Chromosome number, (0) $x = 5$ or 4 , the "mariana" karyotype or its $n = 5$ homologue, or $n = 9$ (1) $n = 4$ or $n = 3$, the "pilosa" karyotype
 3. Chromosome number, (0) $n = 4$ or $n = 3$, the "pilosa" karyotype, or $n = 9$ or $n = 5$ (1) $x = 4$, the "mariana" karyotype
 4. Duration, (0) perennial or biennial (1) annual
 5. Flowering phenology, (0) primarily in late summer and fall, rarely in the spring (1) typically beginning in the spring, often continuing into the fall
 6. Rhizomes/roots, (0) rhizomes (1) taproots
 7. Capitulescence, (0) loosely to compactly corymbose (1) monocephalous
 8. Flowering branch length, (0) relatively short, arising from the upper third of the stem, or the stems monocephalous (1) relatively long, commonly arising from the lower half of the stem
 9. Leaf insertion, (0) clasping or subclasping (1) not at all clasping
 10. Vestiture of peduncles and phyllaries, (0) stipitate glandular (1) glandularity absent or highly reduced
 11. Type A trichomes, (0) terete with thick, papillate walls (1) terete to flattened with thin, smooth walls
 12. Type A trichome length, (0) relatively short, not at all flagelliform (1) all flagelliform, with the distal cells greatly elongated, at least in some species
 13. Phyllary midvein, (0) mostly included within lamina (1) prominently raised-swollen, orange glandular
 14. Phyllary margins, (0) scarious rim narrow or absent (1) scarious rim very broad
 15. Phyllary apex, (0) attenuate or linear-attenuate (1) blunt-acute
 16. Phyllary apex, (0) attenuate or blunt-acute (1) linear-attenuate
 17. Behavior of buds, (0) erect (1) nodding

TABLE 1. (continued).

18. Ray color, (0) yellow, drying yellow (1) yellow or creamy white, drying yellow tinged with red
 19. Ray corolla behavior after stigma receptivity, (0) coiling (1) remaining straight
 20. Sweeping hair shape, (0) narrowly oblong or slightly broadened apically (1) distinctly lanceolate, at least those near the apex
 21. Sweeping hair apex, (0) narrowly oblong to lanceolate, without a sharp point, or narrowly acute with a sharp point (1) broadly acute with a sharp point
 22. Sweeping hair apex, (0) narrowly oblong to lanceolate, without a sharp point, or broadly acute with a sharp point (1) narrowly acute with a sharp point
 23. Elongate crystals in the tissues of the disc corolla throat, (0) present (1) absent or greatly reduced in size
 24. Resin ducts in disc corolla lobes, (0) continuous or absent (1) discontinuous
 25. Radial walls of cells of upper throat of disc corollas, (0) straight (1) broadly sinuate
 26. Achene walls, (0) eglandular, or with thin, barely raised glandular ridges (1) with thick, raised, glandular ridges
 27. Achene shape, (0) narrowly elliptic to oblanceolate in side view (1) obovate
 28. Achene compression, (0) distinctly compressed (1) terete or subterete
 29. Achene nervation, (0) thin, superficial (1) thick, beneath the surface
 30. Pappus insertion, (0) at shoulder rim of achene apex (1) inset from shoulder rim of achene apex
 31. Pappus series, (0) double (1) single
 32. Outer pappus, (0) setae or absent (1) scales
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TABLE 2. Data matrix for *Osbertia*, *Bradburia*, and the diploid species of *Chrysopsis*.

Taxa	Character State							
<i>Heterotheca</i> (HETERO)	00000	100?0	00000	0?000	00000	00000	00	
<i>Noticastrum</i> (NOTICA)	0000?	?1001	11000	0?110	00000	00000	00	
<i>Osbertia</i> (OSBERT)	?0000	01000	10000	00110	00001	00100	10	
<i>Bradburia</i> (BRADBU)	01011	10110	10010	00011	10101	01011	00	
<i>Chrysopsis pilosa</i> (PILOSA)	01011	10100	10010	00011	10101	01011	01	
<i>C. mariana</i> (MARIAN)	10100	00000	11000	00001	00000	01011	01	
<i>C. lanuginosa</i> (LANUGI)	10000	10000	11000	11001	00000	01011	00	
<i>C. godfreyi</i> (GODFRE)	10000	10000	11000	11001	00000	01011	00	
<i>C. floridana</i> (FLORID)	10000	10000	11001	00001	01000	01011	00	
<i>C. scabrella</i> (SCABRE)	10000	10000	11001	00001	01000	01011	00	
<i>C. latisquamea</i> (LATISQ)	10000	10010	11100	00000	00010	11011	00	
<i>C. linearifolia</i> (LINEAR)	10000	10011	11100	00001	00010	11011	00	
<i>C. subulata</i> (SUBULA)	10001	10011	11100	10001	00010	11011	00	

Florida, the present analysis suggests that such an ancestor, derived from Latin American precursors, probably migrated northward into south central and southeastern North America. The initial divergence, which occurred in the south central region, separated the two major lineages. The species of sect. *Chrysopsis* form four main clades. The relationship among them has not been resolved despite a detailed search for potentially useful characters, but on the basis of their karyotype and long flagelliform hairs, these species are united as a group distinct from sect. *Bradburia*. The morphological data suggest that the ancestor to sect. *Chrysopsis* may have been more or less simultaneously fragmented into four lineages.

The base chromosome number of ancestral *Chrysopsis* is most parsimoniously $x = 9$ in the present hypothesis, but the lack of any primitively $n = 9$ species of *Chrysopsis* and the geographic proximity of the closely related *Osbertia* (Nesom 1991b), with its base chromosome number of $x = 5$, suggests that it, rather than *Noticastrum*, may be phyletically coordinate with *Chrysopsis* and that the primitive number for *Chrysopsis* is $x = 5$. If *Osbertia* and *Chrysopsis* are positioned as sister genera, with *Noticastrum* primitive to both, only two steps are added to the cladogram in Fig. 1, both as easily conceivable parallelisms in characters 7 and 18. A study of the karyotype of *Osbertia* will be critical in further assessing its relationship to *Chrysopsis*.

Whatever may prove to be true regarding the base chromosome number for the immediate ancestor of *Chrysopsis*, within the genus the evolutionary attainment of four pairs of chromosomes in *C. mariana* appears to have oc-

curred independently of that in the ancestor of *C. pilosa* and *C. texana*. Even if characters related to chromosomes (characters 1, 2, and 3) are deleted from the analysis, the topology of the resulting cladogram is no different from that in Fig. 1. This supports the hypothesis that the $x = 4$ *pilosa* and the $x = 4$ *mariana* karyotypes are not homologous.

The phylogenetic hypothesis presented here for *Chrysopsis* is similar to the one developed more intuitively by Semple (1981, Figure 3, p. 331). Apart from the general methodology of its construction, without the use of an outgroup for the polarization of character states and without the inclusion of *Bradburia*, Semple's diagrammed hypothesis differs primarily in its indication that *C. pilosa* and *C. mariana* are sister species (based on their reduced chromosome number) and the placement of *C. scabrella-floridana* and *C. lanuginosa-godfreyi* in a single clade (apparently based on geography and what are interpreted here as shared plesiomorphies). The narrative evolutionary scenario for the genus related by Semple (1981) differs from his diagram. In the narrative, he postulated that the divergence of the *latisquamea* lineage and the *scabrella-lanuginosa* lineage from the ancestor of the genus was the first cladistic event, followed by the divergence of the $x = 4$ lineage (including *C. pilosa* and *C. mariana*) from the *scabrella-lanuginosa* lineage. In the narrative, also, he hypothesized that some populations of the immediate precursor of *C. pilosa*, as it migrated from the Florida region toward the Ozark Plateau, became isolated and evolved into *Bradburia*.

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APPENDIX 1. Notes on character variation.

- 1, 2, and 3. Chromosomes: see discussion in text. The scoring relies on data furnished by Semple & Chinnappa (1980b, 1984).
4. Duration: Semple & Chinnappa (1984) observed that the $n = 4$ plants of *Bradburia* lived for 2 1/2 years, as opposed to the strictly annual $n = 3$ ones. This species is scored here as annual, but it would not change the results if it were scored as perennial.
5. Flowering phenology: data from Semple (1981).
6. Rhizomes/roots: some species of *Noticastrum* are rhizomatous, others taprooted; the genus is scored ambiguously, but even if it were not, the topology of the cladogram would not change. The primitive condition of the goldenaster root system is not clear (Nesom 1991a), but *Heterotheca*, which is used as the outgroup in the present analysis, is apparently primitively taprooted.
7. Capitulescence: in *Osbertia* and nearly all species of *Noticastrum* the stems are monocephalous, but some plants of *N. marginatum* (Kunth) Cuatr. produce loose cymes, with several head-bearing branches arising on the upper third of the initial stem. The same is true for *O. bartlettii* (S.F. Blake) Nesom.

Such variants probably reflect the ancestral condition for these two genera, displayed with a release of the suppression of lateral branches.

8. Head bearing branches: in most of *Chrysopsis*, as well as in the genus *Heterotheca*, the capitula are produced on relatively short peduncles originating from a branch point on the upper part of the main stem. In *C. pilosa* and *C. texana*, the peduncles are usually longer and originate from lower portions of the stem.

9. Leaf insertion: in *Bradburia* as well as the three species of the *C. latisquamea* Pollard lineage, the leaves are clearly sessile; in *C. scabrella* Torr. & Gray, *C. floridana* Small, *C. lanuginosa* Small, and *C. godfreyi* Semple, they are clearly clasping or subclasping. Semple (1981) described leaf insertion in *C. pilosa*, *C. mariana*, and *C. scabrella* as sessile, but these species are more similar in leaf base to the clasping leaved species than to the sessile leaved ones.

11 and 12. The smooth, thin walled Type A trichomes that are often lengthened into a tomentose vestiture are the primary feature that distinguishes the *Chrysopsis* lineage from all of the other goldenasters (Semple *et al.* 1980; Nesom 1991a). Type A trichomes in *Noticastrum* are variable in length from species to species, but in some they are minutely flagelliform and form a dense tomentum identical to that of *Chrysopsis* species. The comparatively high degree of variability in vestiture, as well as habit, among the species of *Noticastrum* is perhaps reflective of the ancestral stock of the whole *Chrysopsis* clade. In the cladistic hypothesis offered here, the relatively short hairs of *C. pilosa* and *C. texana* are more primitive than the long flagelliform, tomentum forming hairs characteristic of the other species of *Chrysopsis*.

13. Phyllary midvein: the phyllaries of *C. subulata* Small and *C. linearifolia* Semple are distinctive in their prominently raised-swollen, orange glandular midveins. The midveins of the other species are somewhat variable but none approach the distinctive morphology of these two species.

15 and 16. Phyllary apex: these features are difficult to characterize with precision, but there appear to be two pairs of species, each pair with phyllary apices distinctive from all other species.

17. Behavior of buds: data for *Chrysopsis* from Semple (1981). Comparative data for most of the rest of the goldenaster lineage is lacking, but the buds of the species of *Heterotheca* sect. *Heterotheca* are nodding.

18. Ray color: among the 12-13 species of *Noticastrum*, only *N. acuminatum* (DC.) Cuatr. has rays that are distinctly yellow when fresh. The other species are noted by collectors as having white to dark lavender rays. Upon drying, however, the rays of seven of the eight species I have studied are a densely opaque, dark orangish yellow, sometimes retaining a purplish tinge. The "dry" color of the rays, with a reddish purple tinge, is similar among the other goldenasters only to that in *Osbertia*. Based on these observations and the distribution of other character states in the present analysis, the white

ray color in *Noticastrum* is interpreted here as derived from the primitive yellow rays of the ancestral goldenaster; the yellow rays of *N. acuminatum* have retained the primitive color.

19. Ray corolla behavior after stigma receptivity: the corollas of post-receptive ray flowers in nearly all genera of the goldenaster lineage tightly coil inward, with the adaxial surface exposed. Only in *Noticastrum*, *Osbertia*, *Chrysopsis pilosa*, and *C. texana*, do they remain straight. In the hypothesis here, the noncoiling behavior of first two apparently has evolved in parallel with that of the second two, perhaps reflecting an inherited tendency. In other species of *Chrysopsis* the tendency to coil may be more weakly expressed than in other goldenasters, but it is clear nevertheless. This behavior can be easily observed even on herbarium specimens; I have also observed *C. pilosa* and *C. texana* in the field and in cultivation. Comparative observations for other species are not available, but in *C. pilosa* and *C. texana*, the ray corollas close upwards in parallel at night, forming a narrow pyramid, spreading the next morning.

20, 21, and 22. Sweeping hair shape and apex: in contrast to the rest of the goldenasters, there is a definite tendency in *Chrysopsis* for the sweeping hairs of the disc style appendages to be lanceolate rather than narrowly oblong, at least near the appendage apex. In two pairs of species this tendency is markedly more pronounced than the other species: in *C. texana* and *C. pilosa*, the sweeping hairs are broadly lanceolate to nearly triangular with sharp points; in *C. scabrella* and *C. floridana*, they are linear-lanceolate with sharp points. These two specialized morphologies do not appear to be strictly homologous. Outside of the goldenasters, lanceolate hairs occur in some species of the *Aster* L. lineage, and the sweeping hair apices of some genera of the *Machaeranthera* Nees lineage show the same tendency to be sharp pointed (Nesom in prep.).

23. Elongate crystals in the tissues of the disc corolla throat: relatively large, elongate, straight sided crystals are found in the throat cells of all species of goldenaster except *Chrysopsis texana* and *C. pilosa* (see Nesom 1991a for further details). The corolla throats of *C. pilosa* produce a mixture of stellate "sand" crystals and elongate crystals but the latter are markedly smaller, apparently through reduction, than those in other goldenaster species. *Chrysopsis texana* produces only "sand" crystals.

24. Resin ducts in disc corolla lobes: in the three species of the *latisquamea* lineage, the yellow-orange resin ducts associated with the veins are sharply discontinuous. This is much less pronounced in *C. latisquamea* than in the other two species.

25. Radial cell walls: the difference between the sinuate walls and straight walls can be easily seen in the cells of the upper throat of the disc corollas. Outside of the goldenasters, sinuate walls are particularly characteristic of the disc corolla throats in some groups of *Aster* (Nesom in prep.) as well as related genera.

26, 27, 28, 28, and 30. Achene morphology: the flattened, obovate achenes of *Chrysopsis* (including *C. pilosa* and *Bradburia*) with subepidermal ribbing, truncate apices and inset pappus insertion are distinctive. Raised, orange, glandular ridges occur in the three species of the *latisquamea* lineage and in *C. gossypina*; similar but much thinner and barely raised ridges occur in *Heterotheca* sect. *Heterotheca*, where they appear to have arisen independently as a specialization within that genus. Relatively long achenes with numerous, superficial nerves appear to be primitive within the goldenasters, but the degree of compression is more evolutionarily plastic and less useful in reconstructing phylogeny. The achenes of *Heterotheca* sect. *Ammodia*, for example, are distinctly flattened; those of some species of *Noticastrum* also are strongly compressed, while others are intermediate in compression between *Chrysopsis* and *Osbertia*. In the present analysis, only *Osbertia* is scored as having terete achenes within the *Chrysopsis* lineage.

The achenes of *Bradburia* are strongly 3 sided, at first sight very different from other taxa of *Chrysopsis*, but ray achenes that are slightly but distinctly 3 sided, in exactly the same way as *Bradburia*, are produced by *C. mariana*, *C. scabrella*, and *C. lanuginosa*, although apparently not by *C. pilosa*.

31 and 32. Pappus: *C. pilosa* has an outer series of broad and conspicuous scales. The outer series in *C. mariana* is also more scalelike than the other species of *Chrysopsis* but less pronounced than in *C. pilosa*. The analysis here indicates that the broad wings of the nearly scalelike pair of bristles of the sterile disc achenes in *C. tezana* may be homologous with the scales of *C. pilosa*. The scaly outer pappus in some taxa of *Heterotheca* sect. *Heterotheca* is interpreted to have arisen as a specialization within that genus and in parallel with that in *Chrysopsis*. Among the goldenasters, a uniseriate pappus occurs only in *Osbertia*, where it is clearly derived.